

Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest

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Killer whales (*Orcinus orca*) were found to use different physiographic regions of their habitat in unique ways. Resident whales fed more in areas of high relief subsurface topography along salmon migratory routes, and may use these geographic features to increase feeding efficiency. Transient whales fed in shallow protected areas around concentrations of their prey, harbor seals (*Phoca vitulina*). Whales traveled across deep, featureless areas in moving from one feeding area to another. Whales rested depending on the previous sequence of behaviors and played in open water areas or adjacent to feeding areas. The location of food resources and habitats suitable for prey capture appears to be the prime determining factor in the behavioral ecology of these whales. These patterns of behavior most likely represent cultural mechanisms that have been learned through trial and error experiences leading to successful foraging strategies.

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Les épaulards (*Orcinus orca*) utilisent chacune des diverses régions physiographiques de leur habitat de façon particulière. Les résidents se nourrissent plus souvent dans les zones qui présentent un relief sous-marin accentué et situées le long des corridors de migration des saumons; cela leur permet sans doute d'augmenter l'efficacité de leur chasse. Les épaulards de passage se nourrissent plutôt dans les régions protégées peu profondes, près de concentrations de leurs proies, les Phoques communs (*Phoca vitulina*). Pour aller d'un site d'alimentation à un autre, les épaulards traversent des zones profondes et unies. Selon la séquence de leurs comportements antérieurs, les épaulards se reposent et jouent dans les zones ouvertes ou près des aires d'alimentation. La localisation des ressources alimentaires et des zones optimales de prédation semble constituer le facteur déterminant de l'écologie du comportement de ces animaux. Ces comportements représentent vraisemblablement des mécanismes culturels appris à la suite d'essais et d'erreurs menant à des stratégies efficaces de quête de nourriture.

[Traduit par la revue]

Introduction

Killer whales (*Orcinus orca*) are distributed throughout all oceans (Perrin 1982), but numbers are generally greater at higher latitudes (Matkin and Leatherwood 1986; Norris and Prescott 1961; Perrin 1982) and in areas of high productivity. The seasonal occurrence of killer whales has been correlated with the occurrence and distribution of prey species: southern elephant seal (*Mirounga leonina*) and penguin species (*Eudyptes* sp.) in the south Indian Ocean (Condy et al. 1978); the northern elephant seal (*Mirounga angustirostris*) at San Benitos Island, California (Norris and Prescott 1961); herring (*Clupea harengus*) in the northeast Atlantic (Jonsgaard and Lyshoel 1970); and salmon (*Oncorhynchus* sp.) in the Pacific Northwest (J. R. Heimlich-Boran 1986).

Killer whales are noted for their predation on other marine mammals (Eschricht 1866; Scammon 1874). However, observations of attacks and stomach contents have indicated that killer whales feed on a diverse array of marine vertebrates and invertebrates, including baleen whales, small toothed whales, pinnipeds, fish, sea turtles, birds, and cephalopods (Caldwell and Caldwell 1969; Hancock 1965; Hoyt 1984; Jonsgaard and Lyshoel 1970; Nishiwaki and Handa 1958; Rice 1968; Smith et al. 1981; Steltner et al. 1984; Straneck et al. 1983; Tarp 1979). Because of the wide range of prey items, killer whales have been considered by some to be generalized, opportunistic feeders (Yablokov et al. 1975). A closer examination suggests that individual populations of killer whales may actually specialize on preferred prey for their given area, perhaps even

shifting prey preferences in response to seasonal variations in prey abundances and catchability (Felleman 1986; Felleman et al. 1988). Most detailed accounts of feeding behavior describe groups of killer whales hunting in a coordinated fashion (see review in Würsig 1986) similar to that described for a wolf pack (Mech 1970) and other social carnivores (Kruuk 1972; Schaller 1972). This behavior is dependent on a high degree of communication and coordination within the group (Würsig 1986) and is an important means to increase feeding efficiency on either individual, large marine mammals or large schools of small fish (Felleman 1986).

Killer whales of the inland marine waters of Washington and British Columbia travel in long-term, cohesive groups called pods. All individuals of this population have been photographed and identified by recognition of pigmentation patterns and scars on the dorsal fin and back (Balcomb and Bigg 1986; Balcomb et al. 1980, 1982; Bigg 1982; Bigg et al. 1976; S. L. Heimlich-Boran 1986). Capture photographs from as early as 1965 show that many of the same groups of individuals have been traveling together for over 20 years. There are three apparently isolated communities of whales that inhabit the Washington and British Columbia coasts during the spring to fall: (i) a northern "resident" community inshore of the northern half of Vancouver Island, totalling 12 pods of 135 whales; (ii) a southern resident community inshore of the southern half of Vancouver Island, totalling 3 pods of 79 whales; and (iii) a "transient" community, totalling 15 pods of 47 whales, whose members have been seen sporadically throughout the entire region (Bigg 1982). There are numerous lines of evidence showing distinct behavioral differences between residents and transients in distribution, seasonal occurrence, social organization, acoustic dialects, feeding behavior, and associations with

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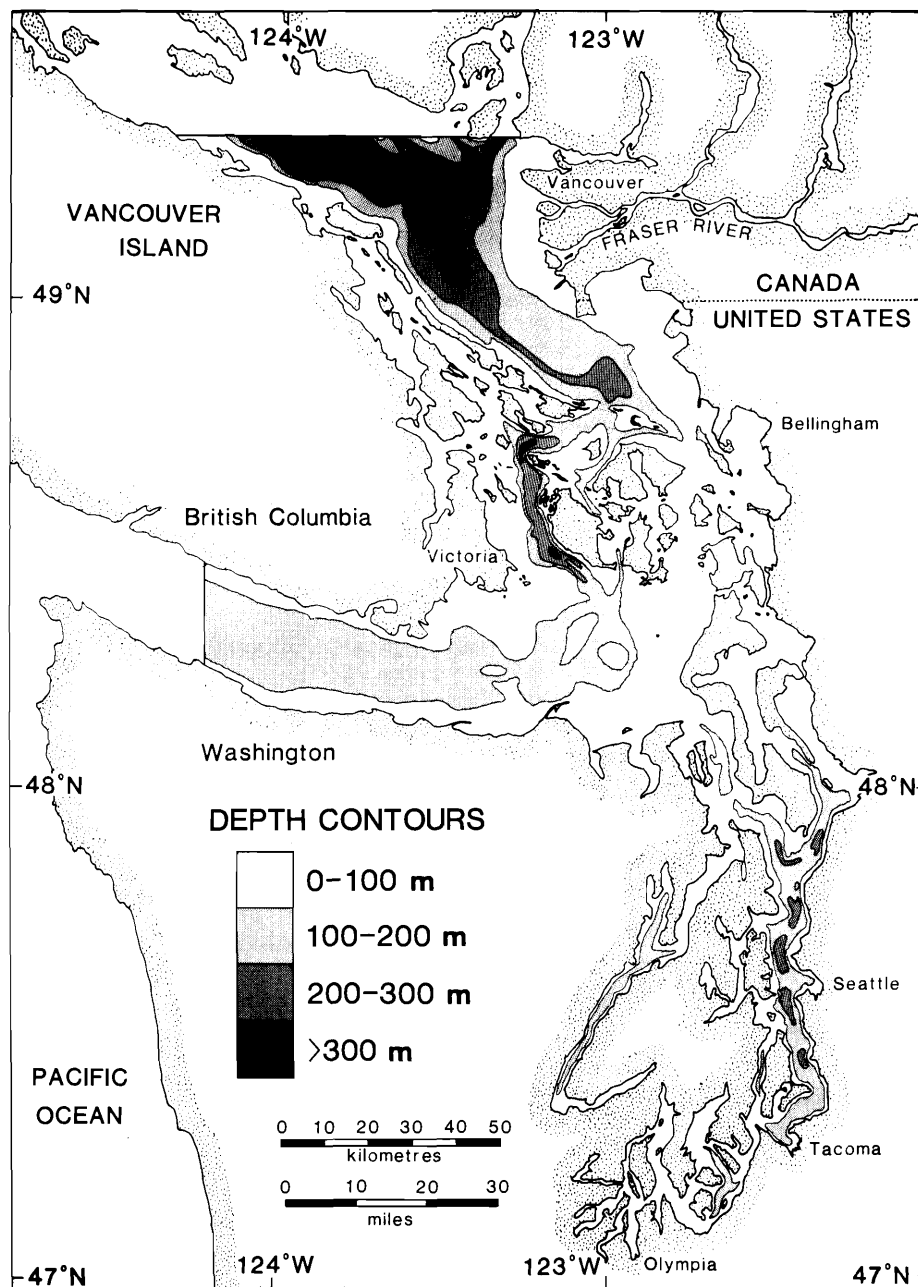


FIG. 1. Bathymetric map of the study area.

tidal currents, as well as suggestions of genetic differences such as dorsal fin morphology and pigmentation (Balcomb and Bigg 1986; Balcomb et al. 1980; Bigg 1982; Felleman 1986; Felleman et al. 1988; Ford and Fisher 1982, 1983). Duffield (1986) has suggested that genetic differences should be apparent in the highly variable chromosomal markers that characterize *Orcinus*, but this work is still in progress. The information to date shows that communities are geographically or socially isolated stocks, implying reproductive isolation between residents and transients.

Here I will examine the habitat-use patterns of resident and transient killer whales in the inland marine waters of Washington and southern British Columbia. I will show how the whales behave differently in different parts of their environment and propose possible reasons for different behaviors. This will show how complex, learned patterns of behavior can be important in the behavioral ecology of these whales.

Methods

Whales were observed in the inland marine waters of Washington and British Columbia (47.0–49.3° N, 122.0–124.2° W) from 1 April 1976 to 31 December 1983. The region is characterized by a highly varied subsurface topography (Fig. 1). Research effort was centered on Haro Strait in the San Juan Islands (Fig. 2).

Whales were photographed and identified from an identification catalog developed in conjunction with M. A. Bigg (Pacific Biological Station, Canadian Department of Fisheries and Oceans, Nanaimo, B.C.). This analysis will deal only with confirmed observations of southern resident and transient pods. The main effort in data collection was to maximize the time with whales, not to determine geographical distribution with randomly collected transect data. Sighting effort was expended year-round, but data collection in winter was limited to only a few observers. The primary assumption of this study was that whale behaviors were sampled randomly. Although behavioral sampling was not random with respect to location and season, the data base was large enough to ensure a random sample of the full

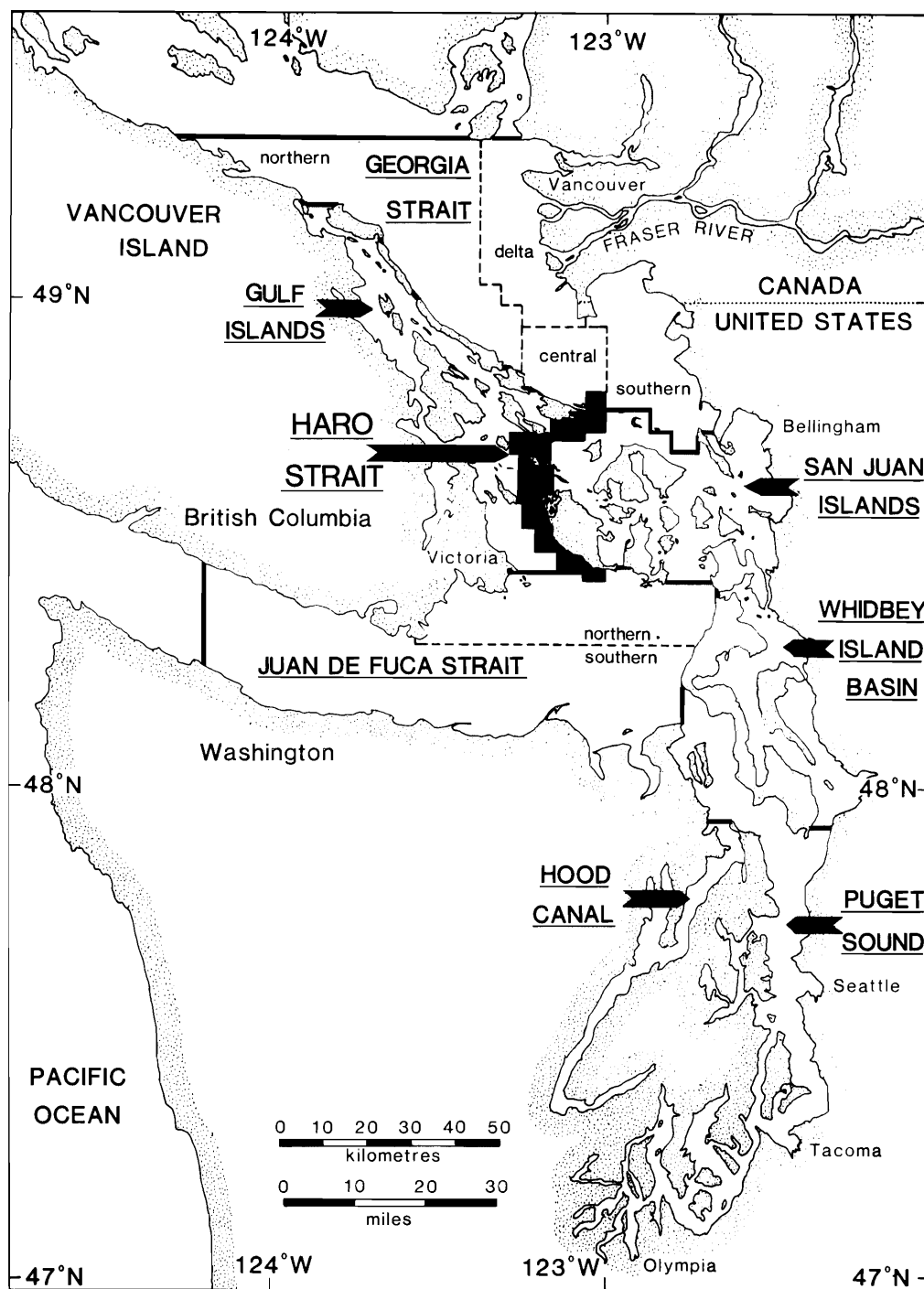


FIG. 2. Map of regions and subregions of the study area.

repertoire of behaviors that occur during the spring to fall season in the study area.

Whales were tracked from 5- to 6-m motorboats or from 10- to 15-m sailing vessels. Each day of tracking an identified pod was termed an "encounter day." Exact whale locations were determined from compass triangulations on nearby shorelines and marked buoys using a Morin Opti2 hand bearing compass. The study area was divided into a grid of 441 quadrats. Each quadrat was approximately 4.6×4.6 km. Whale routes were placed on this grid and quadrat locations were recorded using a 15-min interval scan sampling method (Altmann 1974). The quadrat containing the majority of whales for most of the time period was recorded. This occasionally required that locations of individual whales be averaged to account for the general movement of the entire group.

Behavioral sampling was initially conducted on a continuous basis using the methodology described by Osborne (1986). However, for my analysis, a 15-min sampling regime was overlaid on these data to generate frequency counts of equal intervals, thus standardizing the data and making them comparable with the location data. Behaviors were categorized for the entire group. Behaviors could be accurately recorded at distances up to 500 m. Whales were apparently unaffected by the presence of the research boat; only rarely did they alter their behavior, and even then only for one or two surfacings. Whales were followed for as long as possible. The data were collected by a number of observers; one or more of six skilled observers were present on all encounters, and I was present during approximately two-thirds of the observation hours.

In an attempt to objectively base behavior categories on recogniz-

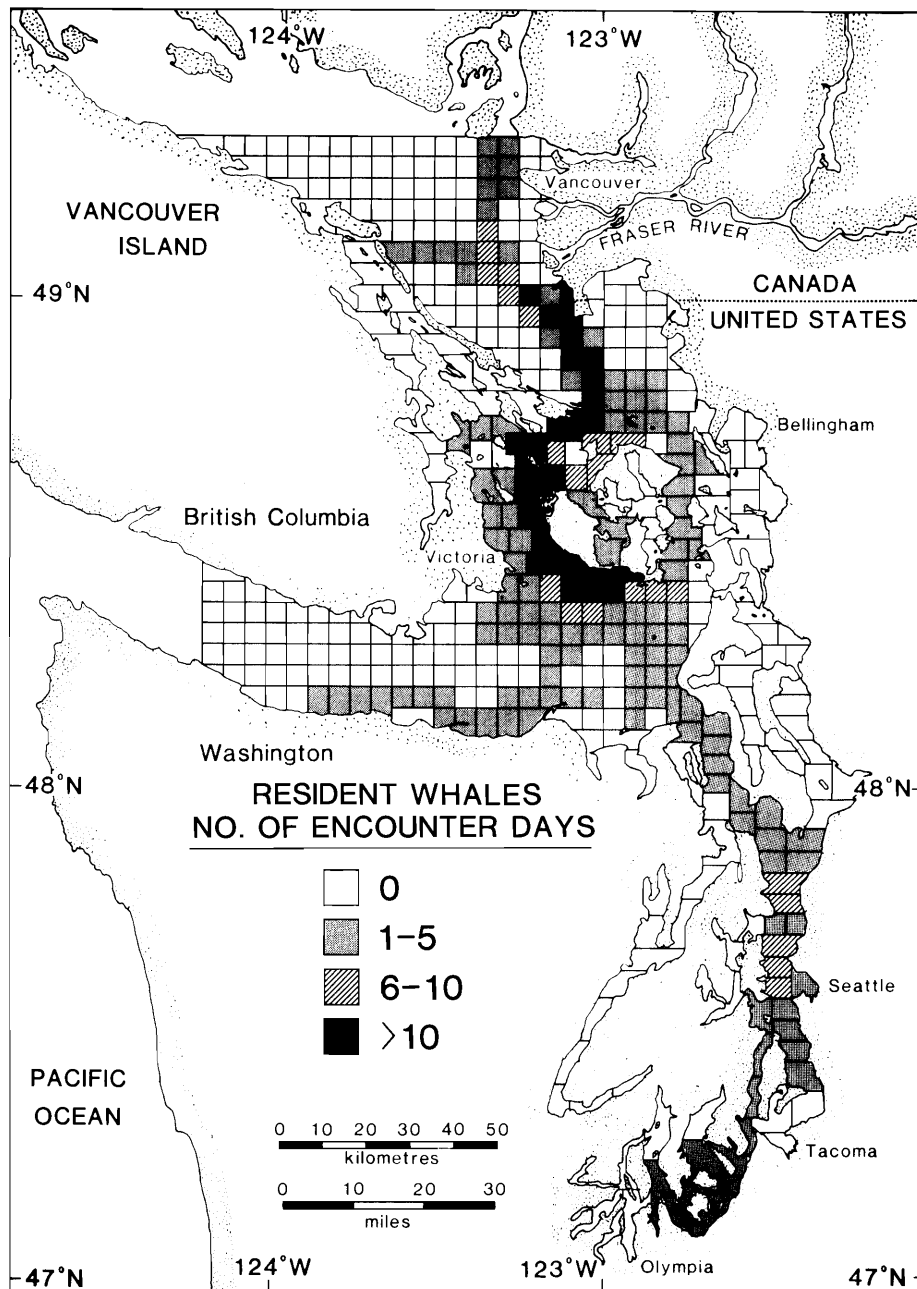


FIG. 3. Distribution map of resident whale encounters.

able surface activities, Osborne (1986) devised a method of combining quantifiable parameters visible at the surface, such as group size, pod composition, spacing of individuals and subgroups, group speed, and directionality of movement. Osborne (1986) analyzed these combinations and defined eight functional behavioral categories: foraging, percussive foraging, milling, travel, percussive travel, rest, play, and intermingling. Much of the following behavior description is a summary of Osborne (1986).

Foraging, percussive foraging, and milling were all considered indicative of feeding and each is thought to represent a unique feeding strategy. Foraging was defined as group directional travel interspersed with occasional breaks of apparently random, nondirectional milling. Whales often traveled in groups wider than long, which is an efficient searching formation (Norris and Dohl 1980a). Percussive foraging had characteristics similar to foraging, travel interspersed with milling, but percussive foraging was performed in much tighter flank formations and was interspersed with coordinated surface splashing behaviors such as lobe-tailing and pectoral fin slapping. Per-

cussive behaviors (specifically the loud noises they create underwater) aid herding behavior of dusky dolphins (*Lagenorhynchus obscurus*) accumulating prey into higher densities, as well as serving a communicatory function to maintain group coordination (Würsig and Würsig 1980). Milling was defined as long-term (longer than 15 min), non-directional swimming by all group members. It appeared to be individual feeding on congregated schools of fish. These behaviors could occur in the order listed in the progression of feeding from searching to collecting to capture or as prey densities increased, but this hypothesis has not been tested to date.

Travel behavior was defined as continuous directional swimming by all group members. Percussive travel was the same behavior interspersed with splashing behaviors and often characterized by high speed (greater than 9 km/h). Animals often traveled in line-abreast formation. This behavior may also serve some coordinated herding function, but it is not interspersed with feeding-related milling, suggesting that prey may be herded over large distances, perhaps aggregated from diverse small groups, before feeding begins. Percussive

behaviors during travelling were often observed in peripheral sub-groups with calves, and may simply represent calf play. On the other hand, percussive behaviors may also serve some social signaling function in dispersed travel groups.

Rest was defined as slow directional swimming or motionless hovering, and was characterized by short, synchronous respiration cycles. Killer whales were silent during this behavior (Hoelzel and Osborne 1986), as has been reported for spinner dolphins (*Stenella longirostris*; Norris and Dohl 1980b).

The final two behaviors may be clumped as socializing behaviors (including "sexual" behaviors). These behaviors seemed to occur year-round, and were not limited to any breeding season. Play consisted of a wide ranging group of individual behaviors usually identified by repeated breaching out of the water by most group members. Play could be distinguished from the percussive behaviors associated with travel and feeding by the lack of any coordinated group formation or direction of movement. Intermingling behavior was a unique behavior, rarely observed, and was characterized by whales from more than one pod congregating in tight, milling clumps in body contact with each other. This behavior was apparently social behavior between two or more pods that occurred when pods met after being apart for some time, and may function similarly to "rallying" groups of spinner dolphins as they group to feed (Norris and Dohl 1980b) or to "greeting ceremonies" of wild dogs (*Lycan pictus*; Estes and Godard 1967).

Whale routes and behavior categories for each encounter were sorted by quadrat and behavior, so that all observations of a given behavior in a given quadrat throughout the study period were pooled. In many cases sample sizes for individual quadrats were too small; observations were then clumped within eight major regions (Fig. 2). To examine differences between the distribution of behaviors in specific, heavily used quadrats (or regions) and the distribution of behaviors for the total study area, χ^2 goodness of fit testing was applied (Zar 1984). The intrinsic null hypothesis was that the behavior distribution for each quadrat should be the same as that for the study area as a whole (i.e., that behaviors were distributed uniformly throughout the area). The occurrence of unique behavior distributions for specific quadrats would imply that the whales were using specific areas for particular behavioral purposes. Adjacent quadrats were tested with heterogeneity χ^2 analysis to examine the statistical validity of pooling observations (Zar 1984). χ^2 tables were then subdivided to locate those behaviors responsible for overall significant differences (Zar 1984). The behaviors with the largest χ^2 values were sequentially removed until the remaining behaviors were not significantly different from the overall behavior distribution. In many cases, more than one behavior was responsible for significant χ^2 values. These could be ranked in order of importance. Also, significance in χ^2 analyses can be due to observations either greater than or less than expected. For this analysis, I will focus on those behaviors that occurred more frequently than expected.

Results

Before presenting results on patterns of behavior and habitat use, it is important to examine the seasonal and geographic distribution of the data base. This places some constraints on the overall applicability of the habitat use results.

Distribution of resident whale observations

Resident whales were observed during 239 vessel encounters for a total of 985.0 h (mean of 4.1 h/encounter) during the study period from 1976 through 1983. They were tracked for 6660 km through 177 (40%) of the 441 study quadrats. The number of encounters per quadrat varied from 1 to 141 (Fig. 3); Fig. 3 shows the distribution of the data base during the study. The Haro Strait region accounted for almost two-thirds of the total observations. This region consisted of 13 quadrats ranging from the southern shores of San Juan Island north along the United States - Canada border for

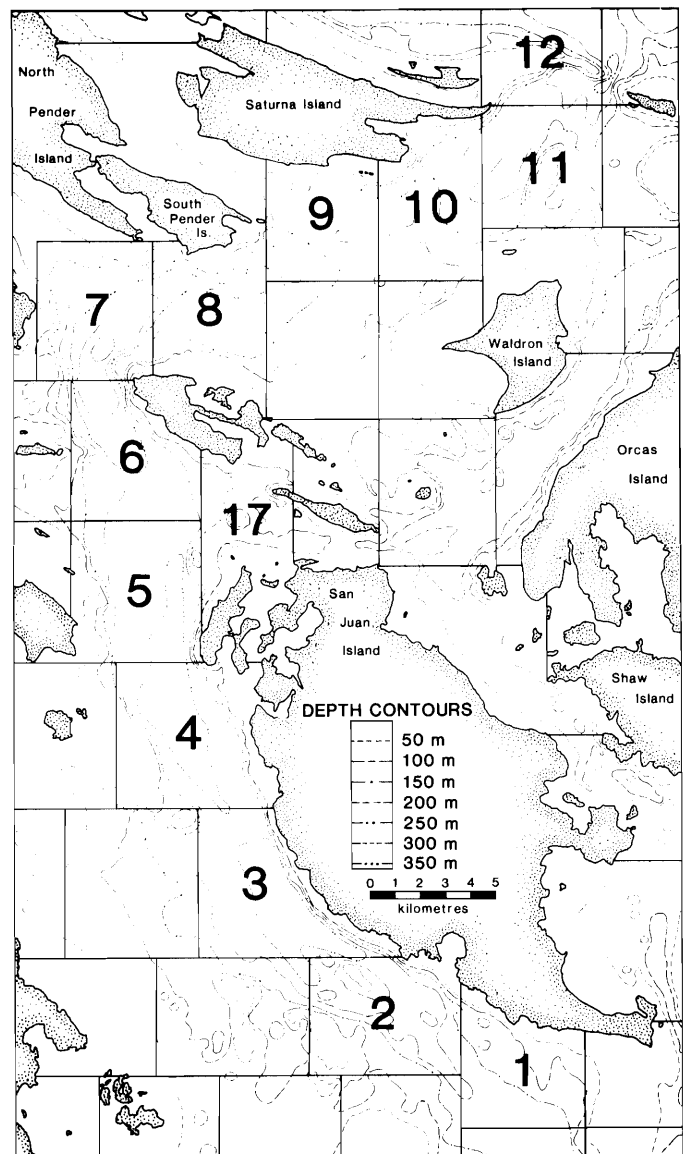


FIG. 4. Bathymetric map of Haro Strait quadrats.

56 km to southern Georgia Strait (Figs. 2 and 4). This strait is also a migratory route for most Fraser River salmon returning to spawn (Groot et al. 1984). Whales were never observed in Hood Canal or the Whidbey Island Basin, although there were occasional sighting reports from those regions. The remainder of the observations were spread nearly equally throughout the other four regions.

Whales were seen in all years of the study period. Two-thirds of the observations were from the first 3 years of the study because of greater effort. Behavior distributions from the individual years were not significantly different from the overall behavior distribution and were homogeneous (heterogeneity χ^2 test, $P > 0.05$), so data from all years were pooled for further analysis.

Whales were seen during all months of the study. However, three-fourths of the observations were in the months of July through September. Although sighting effort was not thoroughly quantified for these vessel observations, there was characteristically a decrease in effort during winter because boats were usually hauled out of the water. However, additional sighting sources (such as shore observations and public

TABLE 1. Counts of behavioral observations for Haro Strait quadrats

Quadrat no.	F	PF	M	T	PT	R	P	IM	Total
1 and 2	106	98	41	44	16	56	46	19	426
3	91	96	44	66	34	57	18	34	440
4	104	121	12	92	36	59	26	26	476
5	45	63	25	38	30	55	40	15	311
17	7	9	11	10	6	22	11	4	80
6	17	57	7	21	31	71	7	3	214
7, 8, 9	27	70	18	50	66	35	30	4	300
10	8	19	0	7	11	10	14	0	69
11	7	13	2	2	6	13	5	0	48
12	10	21	3	4	11	2	14	9	74
Total	422	567	163	334	247	380	211	114	2438

NOTE: Each count represents a 15-min scan sample. Behaviors listed are foraging (F), percussive foraging (PF), milling (M), travel (T), percussive travel (PT), rest (R), play (P), and intermingling (IM).

TABLE 2. Counts of behavioral observations for regions and subregions

Area	F	PF	M	T	PT	R	P	IM	Total
Georgia Strait									
Delta	60	84	10	4	52	2	18	16	246
Central	19	29	4	34	41	0	10	8	145
South	5	0	6	6	0	1	9	10	37
Total	84	113	20	44	93	3	37	34	428
Haro Strait	422	567	163	334	247	380	211	114	2438
San Juan Islands	39	43	5	48	54	57	44	22	312
Juan de Fuca Strait									
North	70	96	22	55	17	44	63	16	383
South	25	19	6	1	7	3	11	0	72
Total	95	115	28	56	24	47	74	16	455
Puget Sound	71	42	50	23	37	39	44	1	307
Total	711	880	266	505	455	526	410	187	3940

NOTE: Each count represents a 15-minute scan sample. Behaviors listed are foraging (F), percussive foraging (PF), milling (M), travel (T), percussive travel (PT), rest (R), play (P), and intermingling (IM).

sighting reports: J. R. Heimlich-Boran 1986) show similar seasonal distribution patterns. In spite of limited winter observations, all of these sources have documented the occurrence of small-scale peaks in killer whale distribution closely timed to the winter occurrence of juvenile and resident salmon as well as migrating steelhead trout (*Salmo gairdnerii*; Felleman et al. 1988). This implies a sufficient level of winter coverage to conclude a predominately spring to fall distribution for southern resident whales in the study area.

Patterns of resident behavior and habitat use

The distribution of behaviors on a percentage basis for the entire study period is shown in Fig. 5. The three feeding behaviors comprised 47% of the whales' time. The two travel behaviors totalled 25% of the time, while rest and the two socializing behaviors occurred with approximately equal frequencies (13% and 15%, respectively). This frequency distribution of behaviors, because of the large and geographically diverse sample from which it came, was accepted as representative for these whales. All other behavior distributions from specific subsamples were compared with it using goodness of fit testing.

I will present the habitat use results for each of the specific behaviors. There were similarities among the areas that shared significant occurrences of particular behaviors. All behavior counts are presented in Table 1 for the 13 Haro Strait quadrats, and in Table 2 for the regions and subregions of the study area.

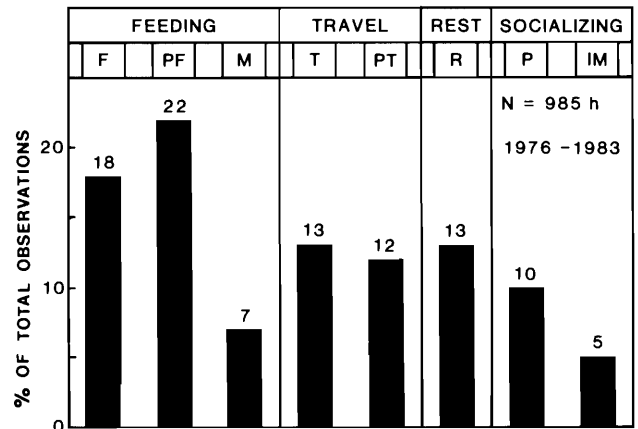


FIG. 5. Behavior distribution for resident whales in all areas. Behaviors listed are foraging (F), percussive foraging (PF), milling (M), travel (T), percussive travel (PT), rest (R), play (P), and intermingling (IM).

The primary areas of increased feeding were in quadrats 1, 2, and 3, and in the regions of the Fraser River delta and Puget Sound. Quadrats 6, 12, and 17 were secondarily important as feeding areas, but will be discussed later in relation to the primary behavior occurring there.

Whales were observed in quadrats 1, 2, and 3 for 216.5 h, or

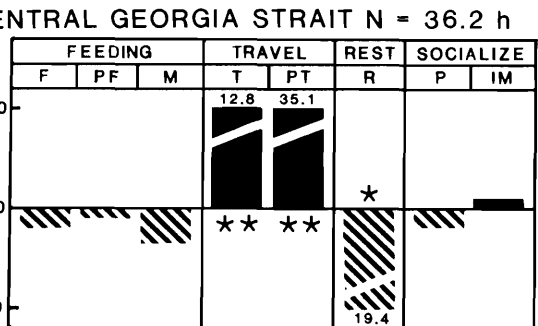
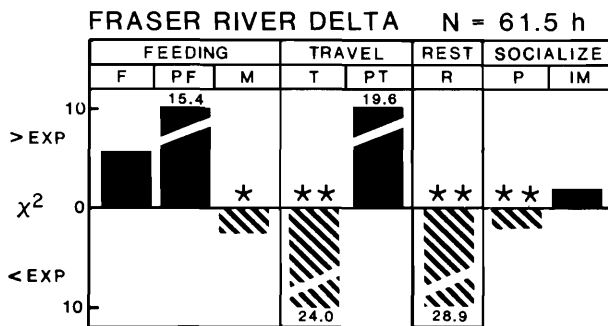
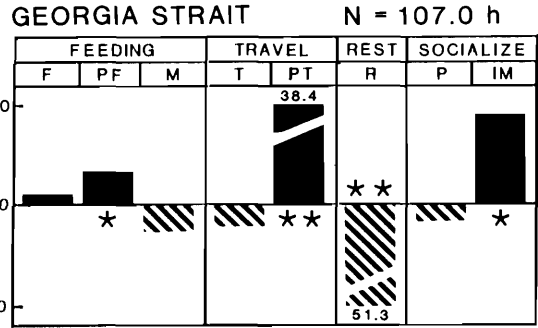
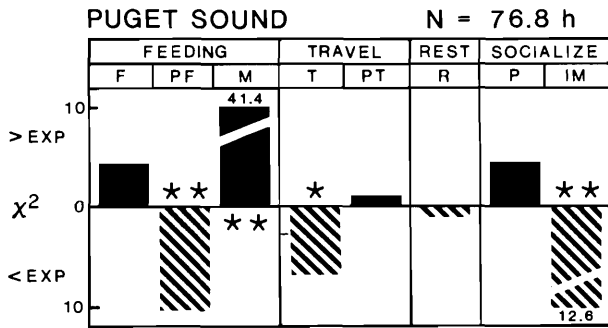
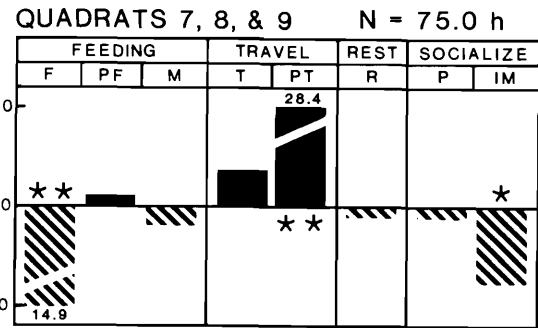
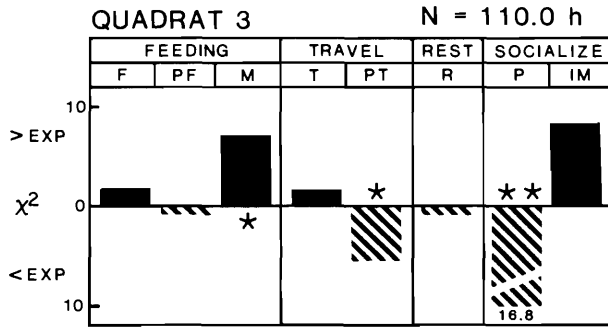
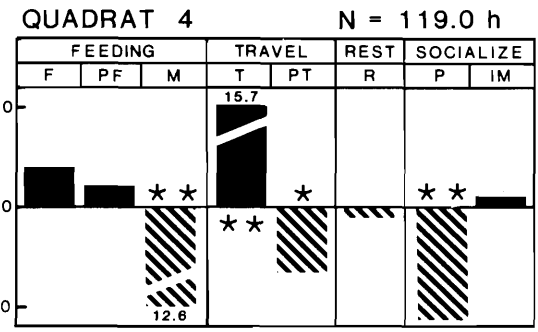
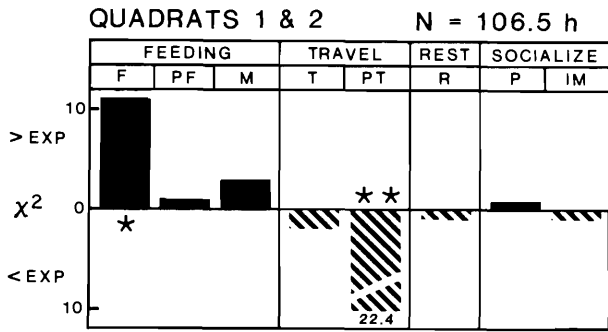


FIG. 6. χ^2 values for feeding areas. F, foraging; PF, percussive foraging; M, milling; T, travel; PT, percussive travel; R, rest; P, play; IM, intermingling. Subdivision of χ^2 significance: *, $P < 0.05$, and **, $P < 0.001$, indicate behaviors responsible for overall χ^2 significance.

FIG. 7. χ^2 values for travel areas. F, foraging; PF, percussive foraging; M, milling; T, travel; PT, percussive travel; R, rest; P, play; IM, intermingling. Subdivision of χ^2 significance: *, $P < 0.05$, and **, $P < 0.001$, indicate behaviors responsible for overall χ^2 significance.

22% of the total sample period (Table 1). Quadrats 1 and 2 were homogeneous in behavior distribution and could be pooled (heterogeneity $\chi^2 = 12.001$, $df = 14$, $P > 0.05$). There were significantly more observations of foraging behavior and a lack of observations of percussive travel ($\chi^2 = 40.9$, $df = 7$, $P < 0.001$) in these quadrats (Fig. 6). These foraging quadrats are located at the southern mouth of Haro Strait along the shores of San Juan Island, and contain some of the most varied bathymetry of the region (Fig. 4). Quadrat 3 had significantly high amounts of milling behavior and a lack

of percussive travel and play ($\chi^2 = 41.0$, $df = 7$, $P < 0.001$; Fig. 6). These three quadrats represent the beginning of a deep trough (200 m) that opens up from the shallower (55 m deep) waters of Juan de Fuca Strait. There are numerous seamounts in quadrats 1 and 2 rising up over 100 m from the sea floor, and complex tidal currents which cause extensive mixing of the waters (Thomson 1981). Quadrat 3 consists of a steep slope that drops to over 200 m deep less than 1 km offshore at San Juan Island (Fig. 4).

Behavior along the Fraser River Delta was characterized by

a lack of milling, travel, rest, and play ($\chi^2 = 99.9$, $df = 7$, $P < 0.001$; Fig. 6). Percussive foraging and percussive travel were the only behaviors that occurred more frequently than expected, though not significantly. However, in Georgia Strait (Fig. 2), percussive foraging did occur significantly more often than expected, although it only ranked fourth in importance (see Fig. 7). Three-fourths of the observations of percussive foraging in Georgia Strait were in the Fraser River delta (although the delta only accounted for 57% of the total observations). Thus, the trend of percussive foraging in Georgia Strait appeared to be important around the Fraser River delta. The Fraser river mouth forms a broad delta 35 km long along the eastern shore of the Strait. There are steep slopes off the mouth of the river which drop over 100 m in less than 2 km (Fig. 1). This is well known as a feeding and lingering area for salmon migrating upstream (Groot et al. 1984).

Milling was the only behavior in Puget Sound (Fig. 2) that occurred significantly more often than expected; percussive foraging, travel, and intermingling were observed much less often than expected ($\chi^2 = 80.2$, $df = 7$, $P < 0.001$; Fig. 6). Whales were observed in Puget Sound for 76.75 h (Table 2). If milling represents an independent mode of feeding on abundant prey, either prey densities in the region were always high (probably of a migratory fish such as salmon) and no cooperative herding was required, or the whales fed on nonschooling fish (such as cod and rockfish) which were best hunted individually. Of course, these options are not mutually exclusive and the whales undoubtedly feed on a variety of prey. However, since I have already shown that the movements of these whales into Puget Sound corresponded to peak salmon fishing catch (J. R. Heimlich-Boran 1986), I would suggest that high salmon densities account for the occurrence of milling behavior in Puget Sound.

Salmon were observed in the vicinity of feeding whales during 26 of 239 encounters, often being pursued by individual whales. Other marine mammals were observed in the vicinity of the resident killer whales during 30 encounters. Of these 30 observations, 2 resulted in observed attacks, once on a harbor porpoise (*Phocoena phocoena*) and once on a Dall's porpoise (*Phocoenoides dalli*). The harbor porpoise disappeared and the Dall's porpoise was last observed with half of its fluke missing. On two other occasions, the killer whales appeared to follow a minke whale (*Balaenoptera acutorostrata*), but no attack was observed. In the remaining 26 cases, the killer whales showed no interest in the other animals. Pinnipeds were observed in the water in 12 instances, usually within 50 m. This suggests that resident whales are not interested in preying on marine mammals. Resident killer whales off northern Vancouver Island also appear to favor salmon as prey, while marine mammals are ignored (Jacobsen 1986; Jefferson 1987; Spong et al. 1970, 1972a).

Travel areas

Travel behaviors occurred significantly more frequently than expected in two areas of Haro Strait: quadrat 4 and pooled quadrats 7, 8, and 9. The subregion of central Georgia Strait also showed a significant increase in observations of both traveling behaviors, as did the overall region of Georgia Strait.

Quadrat 4 was characterized by increased observations of travel and reduced amounts of milling, play, and percussive travel ($\chi^2 = 52.8$, $df = 7$, $P < 0.001$; Fig. 7). Whales were observed here for 124 h over 144 encounters (Table 1). Quadrat 4 is a deep (260 m) and narrow (2 km wide) channel with a

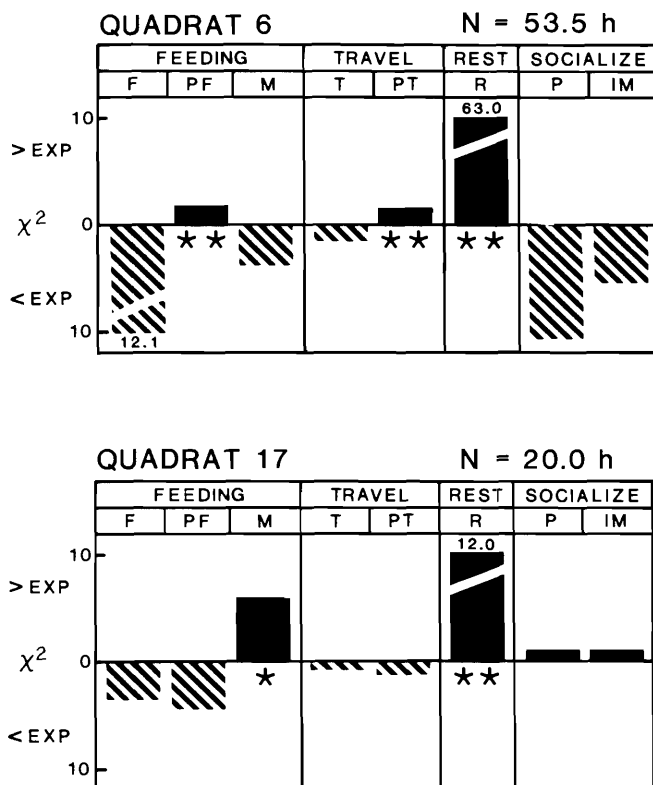


FIG. 8. χ^2 values for rest areas. F, foraging; PF, percussive foraging; M, milling; T, travel; PT, percussive travel; R, rest; P, play; IM, intermingling. Subdivision of χ^2 significance: *, $P < 0.05$, and **, $P < 0.001$, indicate behaviors responsible for overall χ^2 significance.

few reefs along the western border (Fig. 4).

Quadrats 7, 8, and 9 were found to have homogeneous behavior distributions (heterogeneity $\chi^2 = 22.0$, $df = 21$, $P > 0.05$), so data from them were pooled for analysis. Increased observations of percussive travel and a lack of observations of foraging and intermingling characterized this area ($\chi^2 = 55.9$, $df = 7$, $P < 0.001$; Fig. 7). Whales were observed in this area for a total of 75.0 h during 62 encounters (Table 1). Percussive travel was observed during 21 of the 62 encounters, characterized by high speed travel to the northeast. The topography of this region is that of a deep, featureless canyon, sloping from maximum depths of 365 m in quadrat 7 to 125 m in quadrat 9 (Fig. 4).

The subregion of central Georgia Strait (Fig. 2) showed a significant increase in observations of both traveling behaviors along with a lack of observations of rest ($\chi^2 = 74.9$, $df = 7$, $P < 0.001$; Fig. 7). Whales were observed here for 36.25 h (Table 2). The overall region of Georgia Strait was also characterized by increased occurrences of percussive travel, in addition to percussive foraging and intermingling ($\chi^2 = 108.9$, $df = 7$, $P < 0.001$; Fig. 7). This region is a 150 m deep basin with uniform bathymetry between the Fraser River delta and northern Haro Strait (Fig. 1). As soon as whales entered central Georgia Strait from Haro Strait they invariably began traveling rapidly, "porpoising" out of the water. They continued this behavior until they reached the opposite shore of the strait at the feeding area of the Fraser River delta.

Rest areas

Rest occurred significantly more often than expected in two

adjacent quadrats of Haro Strait, 6 and 17 (Fig. 8). Rest was the primary behavior in quadrat 17 ($\chi^2 = 28.0$, $df = 7$, $P < 0.001$). It was observed during 10 of the 32 encounters. Quadrat 6 also had a significant number of observations of rest ($\chi^2 = 99.4$, $df = 7$, $P < 0.001$). Both of these areas also had increased occurrences of feeding. Percussive foraging was observed significantly more often than expected in quadrat 6. Milling occurred significantly more frequently than expected in quadrat 17. In addition, quadrat 6 was characterized by increased observations of percussive travel.

Quadrat 6 is characterized by the sheer cliffs along the eastern shoreline which drop to depths of 270 m a few hundred metres from shore (Fig. 4). At the northern border of the quadrat there is a kelp-covered sill rising almost 200 m in elevation and jutting 300 m into the strait; the top of the sill is 20 m below the surface. Quadrat 17 is ringed by islands and shallow (<100 m deep) channels on three sides and drops to 200 m depth on the western edge along quadrat 6. There is a large kelp-covered seamount rising from 170 to 10 m in the center of the quadrat, as well as a number of other smaller reefs (Fig. 4).

Socializing areas

The social behaviors of play and intermingling occurred significantly more often than expected in two quadrats of Haro Strait, quadrats 10 and 12 (Fig. 4), and in the Juan de Fuca Strait region (Fig. 2). Behavior in quadrat 10 was characterized by significantly more observations of play and a lack of observations of milling ($\chi^2 = 18.4$, $df = 7$, $P < 0.025$; Fig. 9). Whales were observed in this quadrat for 17.25 h during 40 encounters (Table 1). Quadrat 12 was primarily characterized by increased observations of both intermingling and play, along with percussive foraging ($\chi^2 = 26.7$, $df = 7$, $P < 0.001$; Fig. 9). These socializing behaviors occurred during 30% of the 43 encounters in these two quadrats. These quadrats share the physiographic characteristics of feeding areas. There is a prominent kelp-covered sill which juts across the center of quadrat 12. This sill is steep on both the Haro and Georgia strait sides, generating strong upwelling currents at both ebb and flood tides (Thomson 1981). The tidal currents are markedly strong and produce numerous tide rips, eddies, and whirlpools at periods of peak tidal flow (Thomson 1981). In the entire region of northern Haro Strait, whales exhibited behaviors of high activity level, which continued as the whales crossed the shallow sill of quadrat 12. Thus, "play" behaviors in this area may just have been different forms of percussive behavior used to drive fish against the sill for feeding.

Behavior in Juan de Fuca Strait (Fig. 2) was characterized by increased observations of play and a lack of observations of percussive travel ($\chi^2 = 39.2$, $P < 0.001$; Fig. 9). Whales were observed here for 113.7 h. Juan de Fuca Strait is one of the major open water areas of the region.

Distribution of transient whale observations

Transient whales were observed during 18 encounters for 42.75 h (mean of 2.4 h/encounter) from 1976 to 1985. They were observed in 29 of the 441 quadrats of the study area (Fig. 10). Ten of those 29 quadrats (34%) were areas in which resident whales were never observed in almost 1000 h of observation, although the 10 quadrats were all adjacent to quadrats frequented by resident whales. This provides clear evidence of different geographic distributions between transient and resident whales.

The seasonal distribution of the 18 transient whale encounters shows no clear seasonal trends. There were two peaks of

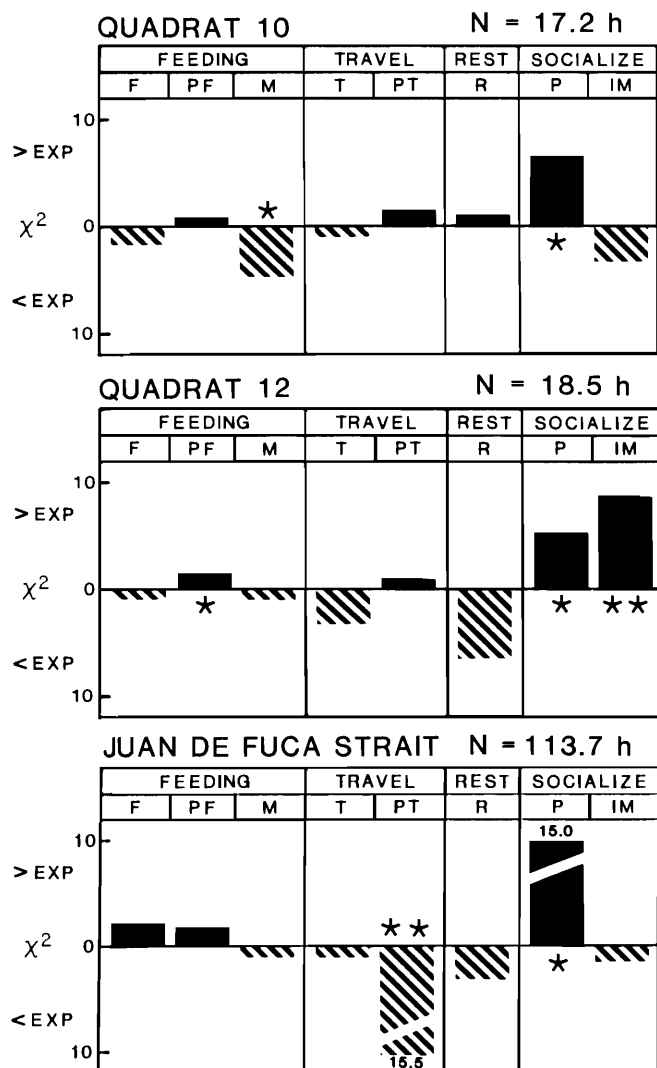


FIG. 9. χ^2 values for socializing areas. F, foraging; PF, percussive foraging; M, milling; T, travel; PT, percussive travel; R, rest; P, play; IM, intermingling. Subdivision of χ^2 significance: *, $P < 0.05$, and **, $P < 0.001$, indicate behaviors responsible for overall χ^2 significance.

observation. Five encounters occurred in the months of March, April, and May. The remaining 13 encounters were in the months of August, September, and October. This is the period of harbor seal (*Phoca vitulina*) pupping in the region (Everitt et al. 1979). Transients were never seen in the months of June and July, a period of increasing resident whale occurrence. Of course, this is still a very limited data set and conclusions must be considered tentative.

Patterns of transient behavior and habitat use

The behavior of the transient whales was characterized by increased feeding behavior compared with that of the resident whales ($\chi^2 = 307.4$, $df = 7$, $P < 0.001$). Feeding represented 81% of the transient whale observations (compared with 47% for resident whales). Travel behavior occurred 12% of the time, rest was observed 7% of the time, and socializing behaviors were never observed. Four of the 18 encounters (2.5 h) included direct observations of feeding on harbor seals. These four observations represented clear examples of marine mammal predation. Areas of seal concentrations were directly approached and searched until prey were found. There were no

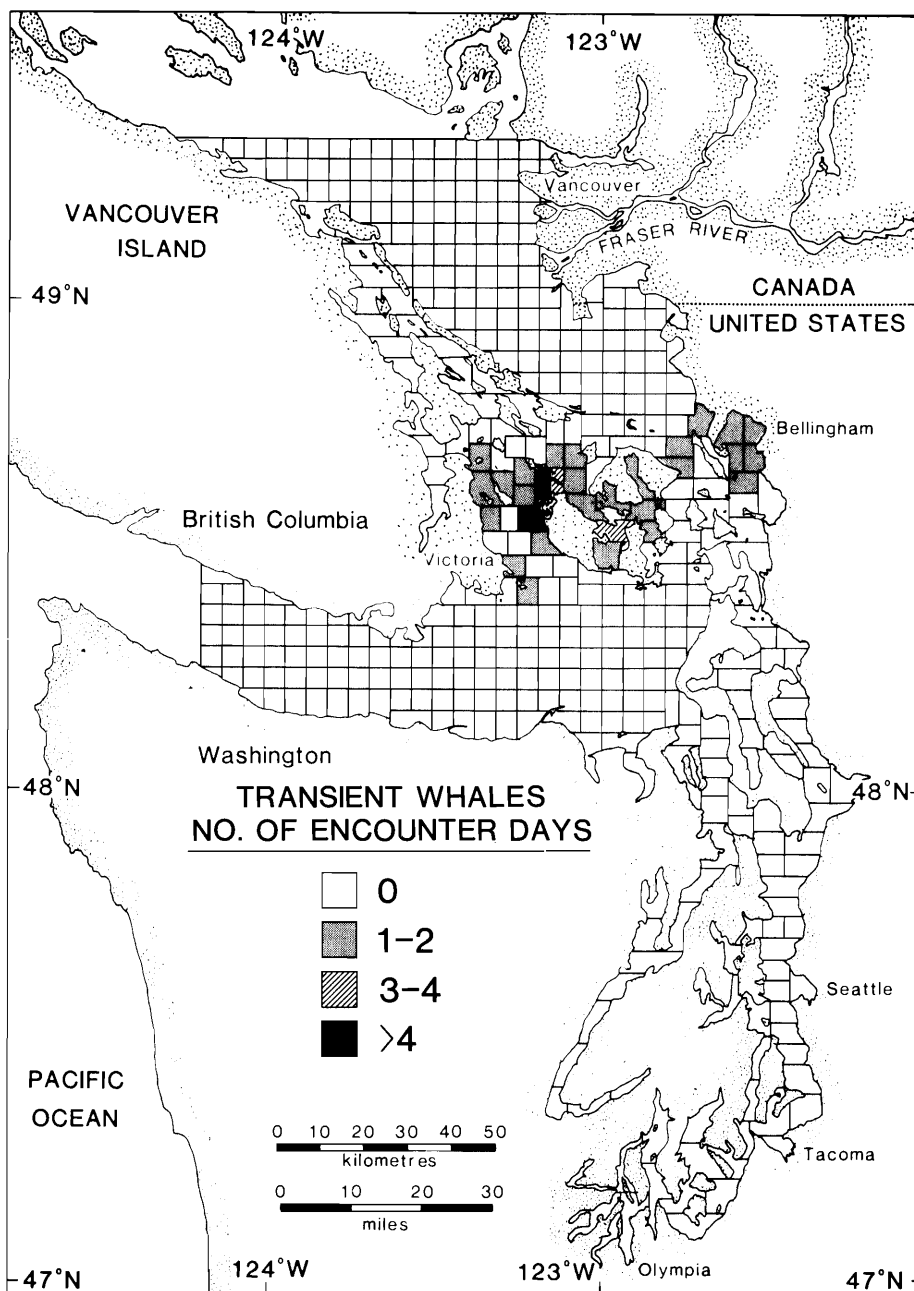


FIG. 10. Distribution map of transient whale encounters.

clear observations of cooperative hunting, although groups of whales occasionally attacked the same seal. On all attacks, the actual kill appeared to be prolonged, perhaps as an instructional activity for young or inexperienced whales, as Lopez and Lopez (1985) have reported for killer whales in Argentina.

The sample size for transient whale behaviors was too small to allow statistical testing for significant geographic variation. However, the quadrats in which transient whales were observed feeding were primarily shallow, nearshore quadrats in areas away from major tidal channels, which in most cases corresponded to harbor seal haul-out areas (Everitt et al. 1979). Harbor seals appear to be an important item in the diet of transient whales.

Transient whales undoubtedly also feed on fish. The occurrences of one pod of transient whales over 3 years in a bay east

of the San Juan Islands have been timed to salmon runs in the Nooksack River. Felleman (1986; Felleman et al. 1988) reported a preliminary analysis of sonar observations of a predominance of large, schooled targets (usually indicative of schooling baitfish) in the vicinity of feeding transient whales. This contrasts with observations of a predominance of large single targets (indicative of salmon) associated with resident pods (Felleman 1986; Felleman et al. 1988). Transients have been observed apparently feeding in kelp, similar to resident whales. Most fish species inhabiting kelp are generally resident and nonmigratory (Matthews and Barker 1983). Their site specificity makes them a predictable resource similar to seals resident at haul-out sites (Felleman 1986). More observations are needed of transient whale behavior before further conclusions can be made.

Discussion

The habitat use patterns of the resident killer whales in Haro Strait appear to be centered around the location of feeding areas. Feeding areas were primarily characterized by high relief bathymetry and the presence of shallow reef areas. These areas are most likely favored feeding areas because of increased prey availability. Evans (1974, 1975) found correlations between the distribution of common dolphins (*Delphinus delphis*) and the location of underwater seamounts off the California coast. The dolphins congregated around these large-scale features even though the shallowest ridge was 2000 m, well below the animals' diving depth. Evans speculated that the animals were able to "hear" the seamounts through passive listening to water noise (as proposed by Norris 1967). Seamounts and kelp-covered reefs are known to provide excellent fish habitat in the Pacific Northwest (Simenstad et al. 1979), especially for residential fish such as rockfish (Matthews and Barker 1983). Numerous fish species feed here on smaller fish and zooplankton supported by the high productivity associated with upwelling generated by the bathymetric features (Boje and Tomczack 1978). Kelp-covered reefs may also provide refuge from predators. Finally, the intensified tidal current regime around these reefs may be attractive to migrating salmon. Salmon traveling through the San Juan Islands tend to move in main current areas and orient along axes of tidal currents (Stasko et al. 1976), such as are found adjacent to these reefs. Felleman (1986) has shown direct correlations between changes in tidal state and killer whale direction changes and behavioral transitions, emphasizing that the whales are very aware of the tides also.

It appears that these habitats are also conducive to collecting prey into higher densities. Some of the effects may be due to physical constraint of the movements of migratory fish. Seamounts and sills restrict the movements of fish and force them to travel closer together, thus making them easier for killer whales to catch. Felleman (1986) suggests that the narrow straits define the home ranges of resident killer whales primarily because of this salmon-collecting effect. However, I also think that the whales actively use these features to herd prey together. The behavioral evidence for this is primarily numerous incidental observations in the vicinity of these features involving flank formations and percussive behaviors. Flank formations aid cetacean predators in scanning large areas for patchily distributed prey resources, while the percussive behaviors cause grouping responses and flight in fish prey (Norris and Dohl 1980a; Würsig 1986). The common physiographic element of all these bathymetric features is a steep underwater slope rising up to within 10 m of the surface. Whales would be able to drive fish towards such barriers to concentrate this prey into denser groups. This could increase capture rates and thus make feeding more efficient. As supplemental evidence, all of these areas are well known to local salmon fishermen as productive fishing grounds.

In contrast to feeding areas, traveling areas were relatively deep water areas with low relief bathymetry. Traveling areas appear to be located between feeding areas, showing that the whales have favored locations for feeding and use travel areas to get from one meal to another. The occurrence of percussive behaviors while traveling in northern Haro Strait and central Georgia Strait may represent herding towards adjacent feeding areas. Prey may be herded over large distances, perhaps aggregated from diverse small groups, before feeding begins. Osborne (1986) showed a sequential relationship between the

percussive behaviors of foraging and travel. Feeding may not occur in the travel areas either because prey are not abundant enough or because the whales are unable to catch prey without the aid of high relief bathymetric features. On the other hand, percussive travel may serve a social signaling function for dispersed travel groups.

The habitat requirements for rest are still unclear. One rest area (quadrat 17) has shallow, protected channels out of the main tidal flow, which may be conducive to resting. Condy et al. (1978) found that killer whales rested in sheltered coves along Marion Island in the Indian Ocean. Humpbacked dolphins (*Sousa* sp.) used a sheltered bay for resting and social activities (Saayman and Tayler 1979). Spinner dolphins (*Stenella longirostris*) off Hawaii rested in a small bay and moved offshore to feed (Norris and Dohl 1980b; Norris et al. 1985). On the other hand, the second resting area (quadrat 6) is primarily a deep, open water area, offering no shallow protected waters. Rest has also been observed in strong currents. During one encounter in quadrat 4, resting was observed while the pod oriented into a strong ebb current. Theodolite tracks showed that the currents were so strong that the whales were actually drifting backwards in the current. In addition, both rest areas were secondarily important as feeding areas and shared feeding habitat characteristics of steep slopes and kelp-covered seamounts. There is currently not enough information about the whales' habitat requirements for rest to draw any conclusions. It could be that the important criterion for rest to occur is the previous sequence of behaviors, not the habitat. Osborne (1986) has shown that rest tended to follow feeding in a significant number of cases. This may explain the occurrence of multiple significant behaviors in the two rest quadrats. Whales may have rested in these areas simply because they went there to feed.

The only habitats that seemed to correspond to the occurrence of socializing behaviors were areas of open water or areas characterized by feeding and other percussive behaviors. There is no apparent reason why intermingling should be tied to specific habitat characteristics since it was primarily dependent on the meeting of separated pods (Osborne 1986), which could occur anywhere. "Play" behavior, as categorized by breaching, may have a wide range of functions, including noise-generating herding behavior or a form of communication between whales. Further conclusions on relationships of play with habitat will have to wait until more is known about the functions of play behavior in these whales.

The location of food resources and habitats suited to prey capture appear to be the prime determining factor in the behavioral ecology of these killer whales, but it is likely that the situation is much more complex than this. Large-brained, efficient predators need not spend all of their time feeding. They undoubtedly have "free time" for socializing, body maintenance activities, or just relaxation which may or may not have specific habitat requirements. Killer whales in the northern resident community have favored "rock rubbing areas" where they linger up to 1.5 h rubbing their bodies on a shallow pebble substrate (Jacobsen 1986). This suggests that foraging is easy in this region.

Cooperative foraging

Behavioral observations during feeding suggest that the whales may use high relief bathymetry as barriers to aid in the collection of prey into higher densities, which should increase feeding efficiency. The whales appear to search for food coop-

eratively by foraging in spread-out subgroups in line-abreast formations, which serves to increase their search area or "school window" (Johnson and Norris 1986). The benefits of "sensory integration" (Norris and Dohl 1980a) provided by such formations are essential in locating and concentrating the patchily distributed food resources of the oceans. The occurrence of percussive behaviors during these periods further suggests the importance of cooperation because these behaviors are used by a group to drive and collect prey (Würsig 1986).

However, from surface observations it appears that the capture of prey by southern resident killer whales is undertaken individually. The behavior category of milling, which represents the most readily apparent feeding behavior (i.e., observations of prey), seems to represent a random pattern of group dispersion. Osborne (1986) has found a good deal of "peripheral" behavior in killer whale groups, suggesting at least the lack of an overt regimen of group coordination. Adult males are often observed foraging independently on the periphery of pods. I have never observed tight, coordinated groups of whales actively surrounding a school of fish while individuals take turns feeding, as Spong et al. (1970, 1972a, 1972b) and Hoyt (1984) have described for northern resident killer whales feeding on salmon. This mode of cooperative foraging has been documented for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Norris and Prescott 1961), and for dusky dolphins (*Lagenorhynchus obscurus*; Würsig and Würsig 1980). In contrast, the killer whales in my study appeared to loosely coordinate their prey searching and possibly prey herding, but then seemed to undertake prey capture on an apparently individual basis.

Of course, there is always the possibility that feeding may be highly coordinated beneath the surface. Hoelzel and Osborne (1986) have shown that vocalization rates of these killer whales are greatest during milling behavior, suggesting the possibility of a high degree of intergroup communication. Würsig (1986), in his review of delphinid foraging strategies, gave examples of how even individually feeding dolphins may be cooperating to some extent. Groups may share information on location and extent of schools of prey. Spinner dolphins breathe synchronously even when feeding independently 50 m or more apart (Norris and Dohl 1980b), suggesting that they may be working together. Similar processes undoubtedly occur in a pod of killer whales feeding on salmon.

All of this must be qualified by the realization that the behavioral categories used here (as for most studies on cetacean behavior) are based on limited observations at the surface of the water. We have no information as to what really goes on beneath the surface. We have no information on success rates of killer whales feeding techniques through real-time monitoring of the whales' encounter and capture rates with different types of prey. I hope that sonar observations will be able to provide this information in the future. A full understanding of the functions of the whales' behavioral repertoire will have to wait until there are more underwater observations of whales directly interacting with their environment. A final note of caution is that all habitats need not serve a specific behavioral function. A knowledge of topography may not allow the prediction of behavior, but it can serve as one clue in the understanding of the behavioral ecology of cetaceans.

Residents and transients

The two sympatric communities of resident and transient whales occur in different areas and feed on different resources in different ways. These findings provide yet one more set of

evidence confirming the very different lives of these two "types" of killer whales.

At this point, we can only speculate as to the origins and sequence of colonization of resident and transient whales in this region. Colonization of the productive, estuarine waters may have required adaptations of oceanic feeding techniques to exploit unique resources. Residents may have been the first to develop efficient methods for feeding on fish, while transients were relegated to the less abundant marine mammal resources. No matter what the scenario, the present situation shows both groups with specialized preferences for feeding on different resources. Residents have movement patterns that follow the distribution of migrating salmon, while transients show equally complex movement patterns which seem designed to exploit harbor seal prey. Thus, both groups exhibit regular patterns of movement that are undoubtedly mediated by memories of locations that have provided previous feeding success (as suggested by Würsig 1986).

The development of specific localized areas for specific behavioral purposes suggests a high degree of tradition and culture in animal societies (Bonner 1980; Wilson 1975). The development of fixed migratory routes in birds and game trails in mammals may represent such traditions (Wilson 1975). The occurrence of such traditional patterns of behavior requires detailed memory, as has been shown for dolphins (Herman 1980). Birds are able to remember locations of hoarded food (Shettleworth 1983), and baboons remember the location of subsurface waterholes during the dry season (Kummer 1971).

Thus, many of the distinctions between residents and transients may be based on learned differences. Acoustic dialects (Ford and Fisher 1982) are most likely completely learned. Learning seems to be an important part of the development of feeding strategies, as evidenced by the observations of Lopez and Lopez (1985) of adult killer whales apparently training young in the capture of pinniped prey. This is undoubtedly a factor in the development of killer whale feeding strategies in the Pacific Northwest.

Are the distinctions described between residents and transients unique to killer whales of the Pacific Northwest during the spring to fall period? Preliminary research in Alaska has found similar distinctions, including group size and prey selection (Hall 1986; Leatherwood et al. 1984). Berzin and Vladimirov (1983) have even proposed a new smaller species of killer whales (*Orcinus glacialis*) from Antarctica that seems to match behaviorally the resident, piscivorous killer whales of the Pacific Northwest. Their *O. orca* behaves similar to the transient killer whales feeding on marine mammals. The distinctions may not require the postulation of a new species, but the point is that killer whales throughout the world may exhibit similar types of behavioral adaptations which are apparent in Pacific Northwest killer whales from the spring to fall. Of course, the winter distribution of all pods is virtually unknown in the Pacific Northwest, and the whales may lead very different lives during this period. There is a need for thorough year-round comparative studies to examine these adaptations.

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- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behavior*, **49**: 227–267.
- BALCOMB, K. C., and BIGG, M. A. 1986. Population biology of the three resident killer whale pods in Puget Sound and off southern Vancouver Island. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 85–95.
- BALCOMB, K. C., BORAN, J. R., OSBORNE, R. W., and HAENEL, N. J. 1980. Observations of killer whales (*Orcinus orca*) in Greater Puget Sound, State of Washington. Final report for Marine Mammal Commission, contract No. MM1300731-7. NTIS PB 80-224728, Springfield, VA.
- BALCOMB, K. C., BORAN, J. R., and HEIMLICH, S. L. 1982. Killer whales in Greater Puget Sound. *Int. Whaling Comm. Rep. Comm.* **32**: 681–685.
- BERZIN, A. A., and VLADIMIROV, V. L. 1983. A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters. *Zool. Zh.* **62**: 287–295.
- BIGG, M. A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Int. Whaling Comm. Rep. Comm.* **32**: 655–666.
- BIGG, M. A., MACASKIE, I. B., and ELLIS, G. 1976. Abundance and movements of killer whales off eastern and southern Vancouver Island, with comments on management. Report available from Arctic Biological Station files, Sainte-Anne-de-Bellevue, Quebec.
- BOJE, R., and TOMCZACK, M. 1978. Upwelling ecosystems. Springer-Verlag, Berlin.
- BONNER, J. T. 1980. The evolution of culture in animals. Princeton University Press, Princeton, NJ.
- CALDWELL, D. K., and CALDWELL, M. C. 1969. Addition of the leatherback sea turtle to the known prey of the killer whale, *Orcinus orca*. *J. Mammal.* **50**: 636.
- CONDY, P. R., VAN AARDE, R. J., and BESTER, M. N. 1978. The seasonal occurrence and behaviour of killer whales, *Orcinus orca*, at Marion Island. *J. Zool.* **184**: 449–464.
- DUFFIELD, D. A. 1986. *Orcinus orca*: taxonomy, evolution, cytogenetics and population structure. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 19–33.
- ESCHRICHT, D. F. 1866. On the species of the genus *Orca*, inhabiting the northern seas. In *Recent memoirs of the Cetacea*. Edited by W. H. Flower. Royal Society, London. pp. 151–188.
- ESTES, R. D., and GODARD, J. 1967. Prey selection and hunting behavior of the African wild dog. *J. Wildl. Manage.* **31**: 52–70.
- EVANS, W. E. 1974. Radiotelemetric studies of two species of small odontocete cetaceans. In *The whale problem: a status report*. Edited by W. E. Schevill. Harvard University Press, Cambridge, MA. pp. 385–394.
- . 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. dissertation, University of California, Los Angeles.
- EVERITT, R. D., FISCUS, C. H., and DELONG, R. L. 1979. Northern Puget Sound marine mammals. Report in partial fulfillment of EPA Interagency agreement No. D6-E693-EN. National Marine Mammal Laboratory, National Oceanic and Atmospheric Administration, Seattle, WA.
- FELLEMAN, F. L. 1986. Feeding ecology of the killer whale (*Orcinus orca*). M.Sc. thesis, University of Washington, Seattle, WA.
- FELLEMAN, F. L., HEIMLICH-BORAN, J. R., and OSBORNE, R. W. 1988. Feeding ecology of the killer whale (*Orcinus orca*). In *Dolphin societies*. Edited by K. Pryor and K. S. Norris. University of California Press, Berkeley, CA. In press.
- FORD, J. K. B., and FISHER, H. D. 1982. Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Int. Whaling Comm. Rep. Comm.* **32**: 671–679.
- . 1983. Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. In *Communication and behavior of whales*. Edited by R. S. Payne. Westview Press, Boulder, CO. pp. 129–161.
- GROOT, C. L., MARGOLIS, L., and BAILEY, R. 1984. Does the route of seaward migration of Fraser River sockeye salmon (*Oncorhynchus nerka*) smolts determine the route of return migration of the adults? In *Mechanisms of migration in fishes*. Edited by J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill. Plenum Press, New York. pp. 283–292.
- HALL, J. D. 1986. Notes on the distribution and feeding behavior of killer whales in Prince William Sound, Alaska. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 69–83.
- HANCOCK, D. 1965. Killer whales kill and eat a minke whale. *J. Mammal.* **46**: 341–342.
- HEIMLICH-BORAN, J. R. 1986. Fishery correlations with the occurrence of killer whales in greater Puget Sound. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 113–131.
- . 1987. Habitat use patterns and behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. M.Sc. thesis, San Jose State University, Moss Landing, CA.
- HEIMLICH-BORAN, S. L. 1986. Cohesive relationships among Puget Sound killer whales. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 261–284.
- HERMAN, L. M. 1980. Cognitive characteristics of dolphins. In *Cetacean behavior: mechanisms and functions*. Edited by L. M. Herman. John Wiley Interscience, New York. pp. 363–429.
- HOELZEL, A. R., and OSBORNE, R. W. 1986. Killer whale call characteristics: implications for cooperative foraging strategies. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 373–403.
- HOYT, E. 1984. Orca: the whale called killer. Camden House Publishing Ltd., Camden Cast, Ont.
- JACOBSEN, J. K. 1986. The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia. In *Behavioral biology of killer whales*. Edited by B. Kirkevoid and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 135–185.
- JEFFERSON, T. A. 1987. A study of the behavior of Dall's porpoise (*Phocoenoides dalli*) in the Johnstone Strait, British Columbia. *Can. J. Zool.* **65**: 736–744.
- JOHNSON, C., and NORRIS, K. S. 1986. Delphinid social organization and social behavior. In *Dolphin cognition and behavior: a comparative approach*. Edited by R. Schusterman, P. Thomas, and F. G. Wood. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ. pp. 335–346.
- JONGSGAARD, A., and LYSHOEL, P. B. 1970. A contribution to the biology of the killer whale, *Orcinus orca* (L.). *Norw. J. Zool.* **18**: 41–48.
- KRUUK, H. 1972. The spotted hyena. University of Chicago Press, Chicago.
- KUMMER, H. 1971. Primate societies: group techniques of ecological adaptation. Aldine-Atherton, Chicago.
- LEATHERWOOD, S., BALCOMB, K. C., MATKIN, C. O., and ELLIS, G. 1984. Killer whales (*Orcinus orca*) of southern Alaska: results of field research 1984. Preliminary report. Hubbs – Sea World Research Institute Tech. Rep. No. 85-175, San Diego, CA.
- LOPEZ, J. C., and LOPEZ, D. 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. *J. Mammal.* **66**: 181–183.

- MATKIN, C. O., and LEATHERWOOD, S. 1986. General biology of the killer whale, *Orcinus orca*: a synopsis of knowledge. In Behavioral biology of killer whales. Edited by B. Kirkevold and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 35–68.
- MATTHEWS, S. B., and BARKER, M. W. 1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish. Bull. **82**: 916–922.
- MECH, L. D. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, Garden City, NJ.
- NISHIWAKI, M., and HANDA, C. 1958. Killer whales caught in the coastal waters off Japan in recent ten years. Sci. Rep. Whales Res. Inst. Tokyo, **13**: 85–96.
- NORRIS, K. S. 1967. Some observations on the migration and orientation of marine mammals. In Animal orientation and navigation. Edited by R. S. Storm. Oregon State University Press, Corvallis, OR. pp. 101–125.
- NORRIS, K. S., and DOHL, T. P. 1980a. The structure and function of cetacean schools. In Cetacean behavior: mechanisms and functions. Edited by L. M. Herman. Wiley-Interscience, New York. pp. 211–261.
- . 1980b. The behavior of the Hawaiian spinner porpoise, *Stenella longirostris*. Fish Bull. **77**: 821–849.
- NORRIS, K. S., and PRESCOTT, J. H. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool. **63**: 291–402.
- NORRIS, K. S., WÜRSIG, B., WELLS, R. S., WÜRSIG, M., BROWNLEE, S. M., JOHNSON, C., and SOLOW, J. 1985. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Southwest Fisheries Center Administrative Report LJ-85-06C. Available from National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA.
- OSBORNE, R. W. 1986. A behavioral budget of Puget Sound killer whales. In Behavioral biology of killer whales. Edited by B. Kirkevold and J. S. Lockard. Alan R. Liss, Inc., New York. pp. 211–249.
- PERRIN, W. (Editor). 1982. Report of the workshop on identity, structure, and vital rates of killer whale populations. Int. Whaling Comm. Rep. Comm. **32**: 617–627.
- RICE, D. W. 1968. Stomach contents and feeding behavior of killer whales in the eastern north Pacific. Nor. Hvalfangst-Tid. **57**: 35–38.
- SAAYMAN, G. S., and TAYLER, C. K. 1979. The socioecology of humpback dolphins (*Sousa* sp.). In Behavior of marine animals; current perspectives in research. Vol. 3. Cetaceans. Edited by H. E. Winn and B. L. Olla. Plenum Press, New York. pp. 165–226.
- SCAMMON, C. M. 1874. Marine mammals of the north west coast of North America. Dover Publications, Inc., New York.
- SCHALLER, G. B. 1972. The Serengeti lion. University of Chicago Press, Chicago.
- SHETTLEWORTH, S. 1983. Memory in food hoarding birds. Sci. Am. **248**: 102–110.
- SIMENSTAD, C. A., MILLER, B. S., NYBLADE, C. F., THORNBURGH, K., and BLEDSOE, A. J. 1979. Food web relationships of northern Puget Sound and the Strait of Juan de Fuca. NTIS EPA-600/7-79-256, Springfield, VA.
- SMITH, T. G., SINIFF, D. B., REICHLER, R., and STONE, S. 1981. Coordinated behavior of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. Can. J. Zool. **59**: 1185–1189.
- SPONG, P., BRADFORD, J., and WHITE, D. 1970. Field studies of the behavior of the killer whale (*Orcinus orca*). In Proceedings of the 7th Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, CA, October 23–24, 1970. Edited by T. C. Poulter. Stanford Research Institute, Menlo Park, CA. pp. 169–174.
- SPONG, P., MICHAELS, H., and SPONG, L. 1972a. Field studies of the behavior of the killer whale (*Orcinus orca*) II. In Proceedings of the 9th Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, CA, October 20–21, 1972. Edited by T. C. Poulter. Stanford Research Institute, Menlo Park, CA. pp. 181–185.
- SPONG, P., SPONG, L., and SPONG, Y. 1972b. Field studies of the behavior of the killer whale (*Orcinus orca*) III. In Proceedings of the 9th Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, CA, October 20–21, 1972. Edited by T. C. Poulter. Stanford Research Institute, Menlo Park, CA. pp. 187–192.
- STASKO, A. B., HORREL, R. M., and HASLER, A. D. 1976. Coastal movements of adult Fraser River salmon (*Oncorhynchus nerka*) observed by ultrasonic tracking. Trans. Am. Fish. Soc. **105**: 64–71.
- STELTNER, H., STELTNER, S., and SEARGENT, D. E. 1984. Killer whales, *Orcinus orca*, prey on narwhals, *Monodon monoceros*: an eyewitness account. Can. Field-Nat. **98**: 458–462.
- STRANECK, R., LIVEZEY, B. C., and HUMPHREY, P. S. 1983. Predation on steamer-ducks by killer whales. Condor, **85**: 255–256.
- TARPY, C. 1979. Killer whale attack. Natl. Geogr. **155**: 542–545.
- THOMSON, R. E. 1981. Oceanography of the British Columbia Coast. Can. Spec. Publ. Fish Aquat. Sci. No. 56.
- WILSON, E. O. 1975. Sociobiology. Belknap Press of Harvard University Press, Cambridge, MA.
- WÜRSIG, B. 1986. Delphinid foraging strategies. In Dolphin cognition and behavior: a comparative approach. Edited by R. Schusterman, R. Thomas, and F. G. Wood. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ. pp. 347–359.
- WÜRSIG, B., and WÜRSIG, M. 1980. Behavior and ecology of the dusky dolphin (*Lagenorhynchus obscurus*) in the south Atlantic. Fish. Bull. **77**: 871–890.
- YABLOKOV, A. V., BEL'KOVICH, V. M., and BORISOV, V. I. 1975. Whales and dolphins, Part II. NTIS JPRS-62150-2, Springfield, VA.
- ZAR, J. L. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.